MADROÑO, Vol. 64, No. 3, pp. 93–98, 2017

VARIATIONS IN SAGUARO CACTUS (*CARNEGIEA GIGANTEA*) SPINE LENGTH IN WET AND DRY PORTIONS OF THEIR RANGE

TALY DAWN DREZNER
Department of Geography, N430 Ross, York University, 4700 Keele Street, Toronto, Ontario, M3J 1P3, Canada
drezner@yorku.ca

ABSTRACT

I sampled spine length in the keystone *Carnegiea gigantea* (Engelm.) Britton & Rose in two northern Sonoran Desert populations where this species is ultimately limited by cold temperatures. I compared spine length (1) between two sites, (2) on north versus south facing sides of plants, (3) by level of shading, (4) by proximity to other potential conspecific competitors, and (5) by presence near sources of surface runoff from which all their water is obtained. Spine length increases, providing thermal protection and reducing photosynthesis, where temperature is more extreme (winter and summer) and where conditions are more xeric. The difference in spine length by direction on plant was much smaller at the more extreme site. Clumped plants that necessarily had increased competition for water but also greater shading were split; at the more extreme site, greater spine shading occurred where water competition was fiercest, while at the less extreme site, greater shading occurred in association with sunlight rather than water.

Key Words: Cactus, *Carnegiea gigantea*, plant-climate relationships, Sonoran Desert.

The benefits of spines are extensive and cacti invest substantial resources to produce them (e.g., Nobel 1988). Our understanding of the function of spines, particularly with regard to climate, is still limited (Steenbergh and Lowe 1983). A variety of explanations have been offered for the purpose of cactus spines. Benefits include protecting water stores from animals (e.g., Stelfox and Vriend 1977, Steenbergh and Lowe 1983), elevating loose cladodes above the hot ground surface (Nobel et al. 1986), water absorption (see Nobel 1983), and protecting the apical meristem from winter freezes by elevating minimum temperatures (Lewis and Nobel 1977, Nobel 1980a, Nobel and Bobich 2002). Spine length and density are related to climate conditions, with increases in length and density observed in a species in more extreme climates and microsites (Yeaton et al. 1980, Nobel 1980b). Cactus surface temperatures are more moderate on spine-covered ridges than on the unspined furrows (Drezner 2011). Spines reflect solar radiation and provide stem shading, reducing maximum surface temperatures in summer (Lewis and Nobel 1977, Nobel 2002). However, spines reduce photosynthesis by reducing CO_2 uptake (Nobel 1977, Lewis and Nobel 1977), which decreases productivity and may be disadvantageous (Nobel 1983), including slowing growth (Nobel 1988).

The keystone cactus *Carnegiea gigantea* (Engelm.) Britton & Rose (Cactaceae, saguaro), provides food, shelter and other benefits to over 100 documented species (Drezner 2014). *Carnegiea* suffers widespread mortality in the colder portions of its range during periodic severe freezing events (Niering et al. 1963), which determine the northern edge of their range (Shreve 1911, Steenbergh and Lowe 1977, 1983). Columnar cactus morphology reflects climatic variations such as increases in diameter with winter rainfall (Drezner 2003a), and narrower stems where winters are relatively warm (Cornejo and Simpson 1997). Ribs are more closely spaced and furrows deeper on the south sides of *Carnegiea* plants compared to north sides (Yeaton et al. 1980). *Carnegiea* ranges further north than *Pachycereus pringlei* (S. Wats.) Britton & Rose, *Lophocereus schottii* (Engelm.) Britton & Rose, and *Stenocereus thurberi* (Engelm.) Buxb., and averages greater spine shading than these taxa (Geller and Nobel 1986). *Carnegiea gigantea* apical spine shading increases with latitude from about 9% at 30.5°N to about 41% at 35°N latitude (Nobel 1980b). Spines and pubescence protect meristematic tissue extending the range of *Carnegiea* and other columnar cacti northward (Nobel 1980a, b). Stem shading by spines increases with elevation for other cacti such as *Cylindropuntia acanthocarpa* (Engelm. & J. M. Bigelow) F.M. Knuth (Nobel and Bobich 2002). While variations in spine morphology may be genetic, the variability observed even over small distances (e.g., Yeaton et al. 1980) suggests that phenotypic plasticity in spine length likely reflects changes in local environmental conditions. The importance of such morphological adaptations will increase with climate warming and range readjustments.

The purpose of this study is to assess spine length at a given site across a variety of microenvironmental conditions, i. e., shade, proximity to competing individuals, presence near surface water (runnels) and north versus south sides of plants, to assess variation in spine length in two different populations. Differences in spine length associated with surface water, shade, orientation and proximity to conspecifics will be compared in a dry, more sparse

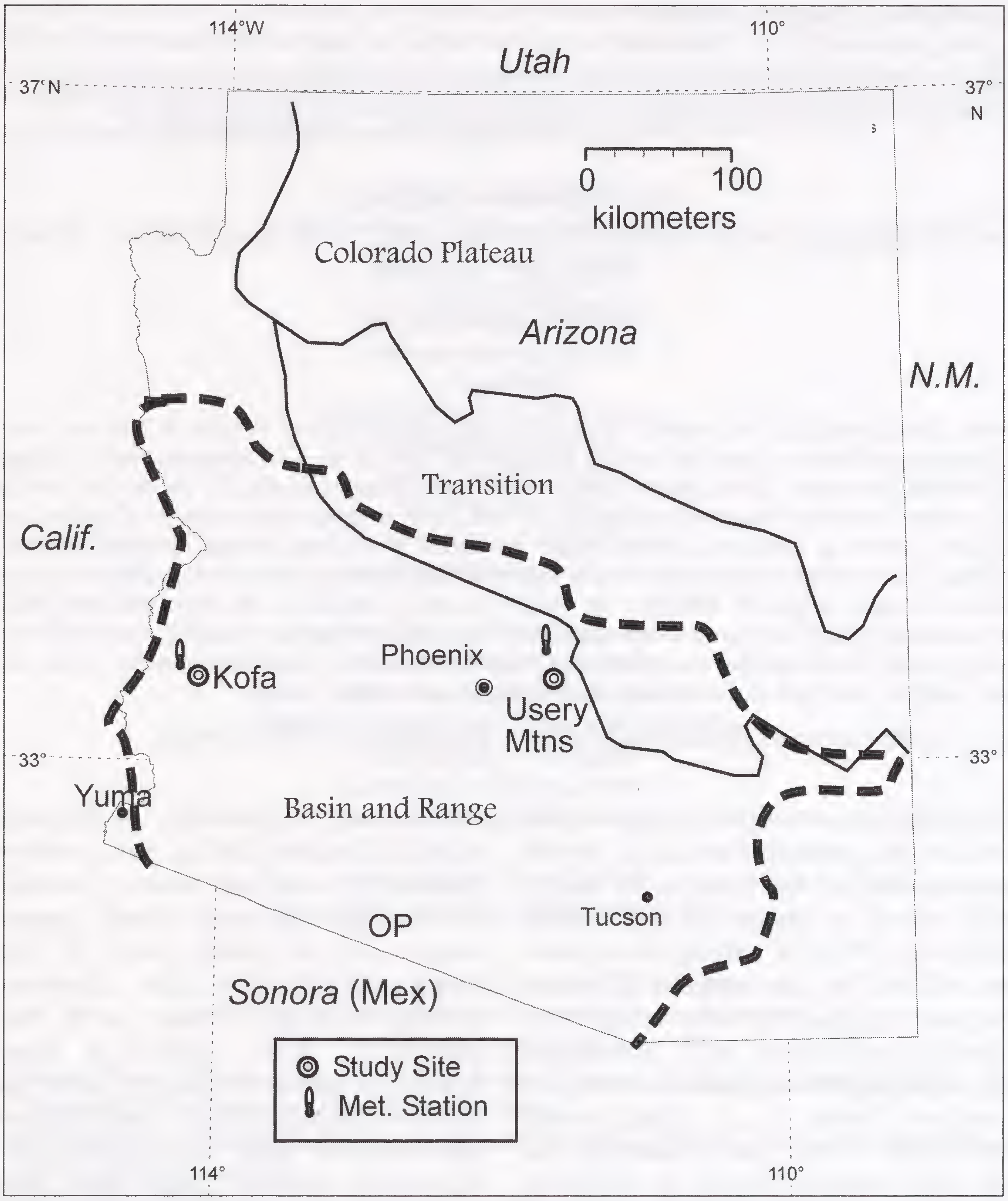

FIG. 1. Locations of the two study sites, Kofa and UM, along with the meteorological stations used (the Quartzsite station is about 16 km from Kofa, Bartlett Dam is about 37 km from the UM site). The dashed line represents *Carnegiea*'s entire United States range. The location of Organ Pipe Cactus National Monument is provided for reference (OP). Physiographic regions (Basin and Range, Transition, Colorado Plateau) from Rasmussen (2006, and references therein).

population in the west and in a wetter and more vegetatively lush population in the eastern Sonoran Desert to determine regional variation. Intraspecific competition for water and proximity to surface water channels are important as they represent the availability of water in a xeric ecosystem.

MATERIALS AND METHODS

Study Sites

The Kofa site (33.534°N, 114.165°W) is west of the western boundary of the Kofa National Wildlife Refuge at an elevation of 400 m above sea level, in the Lower Colorado River Valley subdivision of the Sonoran Desert (Shreve 1951, Turner and Brown 1994, Fig. 1). The Usery Mountains (UM, 33.487°N, 111.612°W, elevation about 650 m) are part of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951, Turner and Brown 1994). The northern Sonoran Desert, where both populations are found, exhibits an east to west gradient in elevation (decreasing towards the Colorado River to the west), which is intertwined with a precipitation gradient (higher precipitation totals to the east) and a pH gradient (lower pH to the east) among other soil gradients over the region (Medeiros and Drezner 2012). Both sites are topographically flat (Kofa about 1.2%, UM about 3.0%; Drezner 2003a).

Data for the Quartzsite meteorological station (#026865) near Kofa (Fig. 1) show that minimum temperatures in January average 2.7°C, while the Bartlett Dam meteorological station (#020632) near the UM site shows that minimum January temperatures average 4.6°C. By comparison, mean maximum July temperatures are 42.7°C near Kofa and 40.6°C near the UM site. The Sonoran Desert

TABLE 1. Statistical results and means. Sample size (n) for each t-test is given along with the mean length (mm) of the spines in that group (L), and the standard deviation (SD). The two sites are the Usery Mountains (UM) and Kofa sites. Other abbreviations include: north (N) and south (S) facing spines on the plant, and all north and south facing spines together (all spines). Other groupings include plants with other plants in close proximity (Clump), and those without nearby competitors for water (No Cl), high and low shaded plants, and plants in runnels, and not accessing runnels (No Run).

Site	Variable	n	L	SD	P
Between-site comparisons (t-tests)					
UM	S facing spines	51	67.8	11.8	
Kofa	S facing spines	51	67.0	11.5	0.74
UM	N facing spines	51	61.3	10.1	
Kofa	N facing spines	51	65.3	10.6	0.0495
UM	all spines	102	64.5	11.4	
Kofa	all spines	102	66.2	11.0	0.29
Within-site comparisons (paired t-tests)					
Kofa	N facing spines	51	65.3	10.6	
Kofa	S facing spines	51	67.0	11.5	0.19
UM	N facing spines	51	61.3	10.1	
UM	S facing spines	51	67.8	11.8	<0.001
Within-site comparisons (t-tests)					
Kofa	Clump	16	71.7	14.2	
Kofa	No Cl	86	65.1	10.1	0.029
UM	Clump	16	57.0	9.5	
UM	No Cl	86	65.9	11.2	<0.01
Kofa	High Shade	32	68.2	13.1	
Kofa	Low Shade	70	65.3	10.0	0.22
UM	High Shade	38	63.6	12.3	
UM	Low Shade	64	65.0	10.9	0.55
Kofa	Runnels	60	65.4	11.8	
Kofa	No Run	42	67.2	9.8	0.43
UM	Runnels	54	62.0	9.7	
UM	No Run	48	67.4	12.6	0.017

receives rainfall from extratropical cyclones in winter while monsoon-driven convective thunderstorms provide rainfall in summer (Carleton 1986, 1987, Sheppard et al. 2002). Mean January, July, and annual rainfall are 13 mm, 12 mm, and 128 mm, respectively in Kofa and 40 mm, 28 mm, and 341 mm, respectively, in the Usery Mountains. Thus, the climate in Kofa is cooler in winter, hotter in summer, and more arid than the Usery Mountains. The vegetation reflects these climate differences, with 7% vegetation cover at Kofa compared with 31% in the Usery Mountains (Drezner 2003b). There are 22 *Carnegiea* per ha at the Kofa site and 60 *Carnegiea* per ha at the UM site (Drezner 2006).

Field Methods

Collection was limited to plants between 2–4 m in height because spines shorten over time due to abrasion (Yeaton et al. 1980). Because spine shading decreases with stem height (Nobel 1980a), results would be biased and unreliable if the full height spectrum was used. At each site, collection began with the first arbitrary plant and continued to each *Carnegiea* individual encountered after ($n = 51$ at each site). Following Yeaton et al. (1980), the longest (typically central) spine was measured on each plant at a height of 1.5 m on the north facing side and then on the south side. If the *Carnegiea* individual was in close proximity to at least one other cactus where some competition for water and/or root interaction would occur, a clump designation (=yes) was assigned to those plants. Assessment criteria included distance to the proximal cactus relative to plant height, as *Carnegiea* roots extend laterally away from the plant as far out as the plant is tall (Cannon 1911). Because of the natural clumped distribution of the species resulting from establishment around nurse plants, such identifications are typically clear. Because *Carnegiea* derive all their water from surficial sources (McAuliffe 1984, McAuliffe and Janzen 1986), plants were classified as in a runnel (area of concentrated surface runoff) thus gaining access to greater amounts of water, or on the intervening area (=no runnel). Degree of shading of the plant was assessed as little to no shade (low), and moderate to high (high) shade. This distinction between high and low shade was made in the field. Plants with large nurses or proximal vegetation blocking substantial light were classified as high shade.

Statistical Methods

The Shapiro-Wilk test was used to ascertain which variables deviated significantly from a normal distribution. Three t-tests were used to compare south-facing spines between the two sites, north-facing spines between the two sites, and all spines between the two sites (Table 1). Next, paired t-tests assessed any difference in length of north- versus south-facing spines at Kofa, and then repeated for the Usery Mountains. North and south aspect data were combined and t-tests were run to assess differences in spine length for clumped plants and plants not proximal to other potentially competing cacti (repeated for both sites). T-tests were run for low and high shade plants, and then for plants in and out of runnels at each site. The correlated Bonferroni technique was applied to the results to correct for type I errors associated with running multiple tests (Drezner and Drezner 2016).

RESULTS

Results of the Shapiro-Wilk normality tests showed that Kofa-north, Kofa-south, and UM-south did not deviate from normality at $P < 0.05$, and UM-north at $P < 0.01$. At the UM site, spines were significantly longer to the south (north: 61.3 mm, standard deviation [SD] of 10.1 mm, south: 67.8, SD 11.8, $P < 0.0001$). Clumped plants at UM had shorter spines (57.0, SD 9.5, unclumped 65.9, SD 11.2, $P = 0.0037$), and plants in runnels had shorter spines (62.0, SD 9.7 in runnels, 67.4, SD 12.6 outside of runnels, $P = 0.0169$, Table 1, Fig. 2). At Kofa, clumped plants had longer spines (71.7, SD 14.2)

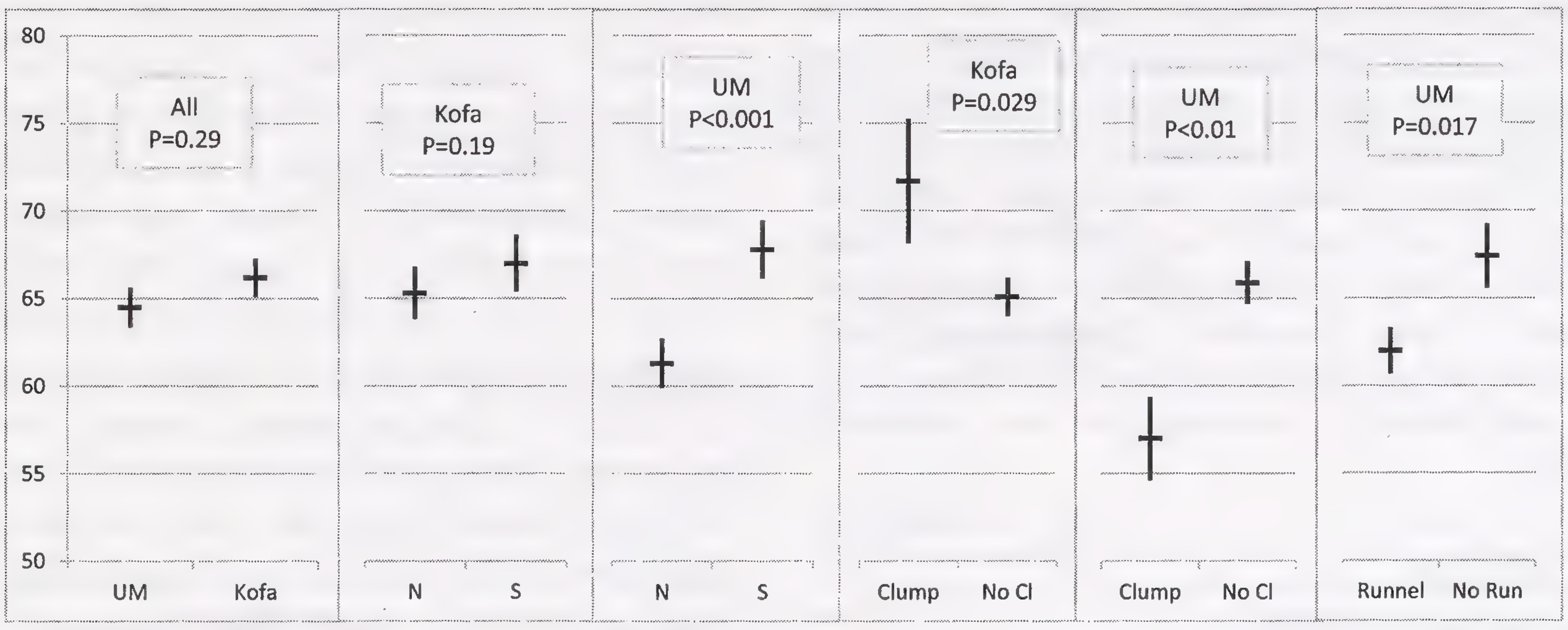

FIG. 2. Mean and standard errors of selected results including spine length (in mm on y-axis) comparing north (N) and south (S) sides of plants, plants in close proximity to other plants (Clump), and plants without potentially competing cacti nearby (No Cl), as well as comparing spine length on plants in and out of runnels (Runnel, No Run).

than unclumped plants (65.1, SD 10.1, P = 0.029), and north-facing spines at Kofa (65.3, SD 10.6) were longer than those at the UM site (61.3, SD 10.1, P = 0.0495). The correlated Bonferroni technique confirmed that all the results are statistically significant (Table 1).

DISCUSSION

Because *Carnegiea* apical spine shading increases to their northern range boundary, phenotypic plasticity in spine expression has been suggested (Nobel 1980b, Nobel 2002). Spines create a boundary layer around the plant, which moderates temperatures (Lewis and Nobel 1977, Drezner 2011). At the UM site, I found that south-facing spines were longer than north-facing spines (with the same trend at Kofa, though not significant). Plants also retain south, sun-facing spines more (Evans et al. 1994). Yeaton et al. (1980) found north-south differences in spine length only on slopes (versus topographically flat populations), which they attributed to greater water stress. However, *Carnegiea* can have faster growth rates on slopes than in topographically flat populations, which are associated with greater water uptake (Donnermeyer and Drezner 2012), so this assertion is variable.

Spine lengths are highly variable across and within populations. Compared to other published information, the variability in length observed here is confirmed. Average spine lengths (around 6.5 cm) are higher than the values reported by Yeaton et al. (1980) at Organ Pipe Cactus National Monument (5.76–6.29 cm averages; they list these values, presumably erroneously, as mm). Britton and Rose (1937, p. 164) identify spines as "often 7 cm long." Variability in length may even be related to rainfall during the summer growing season or other factors influencing growth and health (Steenbergh and Lowe 1977).

Aridity, sunlight and high temperatures promote spine growth and coverage (Lewis and Nobel 1977, Yeaton et al. 1980, Nobel and Bobich 2002, Majure and Ervin 2008, Drezner 2011). Kofa is hotter in summer, colder in winter, and drier than the UM site, and although not statistically significant, spines are longer at Kofa on average. South facing spines are similar at both sites, but north-facing spines are longer at Kofa (thus closing the N-S gap and yielding statistically non-significant results with comparable standard deviations) than at the UM site. At the UM, plants away from areas with concentrated drainage have longer spines, suggesting that longer spines are beneficial where less water is available. Thus, greater solar exposure promotes longer spines, as does reduced available surface moisture, following expectations of a species living in the low water, high summer temperature conditions found in the desert. The more extreme conditions may make spine length more consistent at Kofa than at the wetter UM site, where N facing spines and spines on plants in runnels are significantly shorter. The trend at Kofa is the same by direction and runnel access, but the difference is smaller and thus not statistically significant. Spines may be more important in the more extreme site, especially in otherwise less critical areas (N side, in runnels). Further, spine directionality differences would be less important on winter nights, providing protection in all directions in the colder Kofa. Cacti in colder sites often exhibit greater apical spine coverage (Nobel 1980c).

For clumping, results were significant at both sites but reversed. Clumping affects insolation receipt and water. Plants in close proximity cast shade, which is expected to reduce the need for spine coverage, but they increase competition for water (McAuliffe and Janzen 1986). At arid Kofa, plants in close proximity had longer spines, even with the increase in shade, a reflection of the aridity and relative marginality of this site. At the UM site, which receives nearly three times the amount of rainfall, the clumped plants (with increased shading) have shorter spines; the greater rainfall at the UM site appears adequate to compensate for the effects of intraspecific competition for water. Competition for water may reduce resource investment into spines (Nobel 1988) or alternatively, light limitation in a clumped setting reduces the need (or is disadvantageous) for spines that also cast shade. Spines reduce photosynthesis in cacti (Nobel et al. 1991). Unclumped plants receive more insolation, and they compensate with longer spines.

The observed patterns in spine length suggest that where conditions are more extreme (more extreme seasonal temperatures, greater aridity), spine length increases, reducing photosynthesis and providing thermal protection. The more extreme site had more even spine lengths to the north and south (for example), seen primarily as longer spines in the direction away from the sun. At both sites, sun-facing spines were still longer, and generally large variability in spine length occurs within and across sites. Clumped plants that necessarily had increased competition for water but also greater shading were split; at the more extreme site, greater spine shading occurred where water competition was fiercest, while at the less extreme UM site, greater shading occurred in association with sunlight rather than water. The ability to adapt morphologically to changing conditions contributes to species success with changing environmental conditions. *Carnegiea* is likely to shift northward with warming climate (Rehfeldt et al. 2006) and the great variability in spine length, particularly in the two populations considered here which are towards the northern edge of the species' modern range, will be beneficial for *Carnegiea* as it adjusts to changing conditions. This includes range expansion into previously uninhabited areas as its range extends northward, as well as coping with increasing heat loads.

ACKNOWLEDGEMENTS

I thank Barbara Trapido-Lurie for assistance with the map.

LITERATURE CITED

BRITTON, N. L. AND J. N. ROSE. 1937. The Cactaceae. Descriptions and Illustrations of Plants of the Cactus Family, Volume 2. Second Edition. Dover Publications, New York, NY.

CANNON, W. A. 1911. The root habits of desert plants. Publication No. 131. Carnegie Institute of Washington, Washington, D.C.

CARLETON, A. M. 1986. Synoptic-dynamic character of "bursts" and "breaks" in the South-West U.S. summer precipitation singularity. Journal of Climatology 6:605–623.

———. 1987. Summer circulation climate of the American Southwest, 1945–1984. Annals of the Association of American Geographers 77:619–634.

CORNEJO, D. O. AND B. B. SIMPSON. 1997. Analysis of form and function in North American columnar cacti (tribe Pachycereeae). American Journal of Botany 84:1482–1501.

DONNERMEYER, C. J. AND T. D. DREZNER. 2012. Cohort establishment on slopes: growth rates, demographic patterns, and the relationship to volcanic eruptions. Journal of Arid Environments 76:133–137.

DREZNER, T. D. 2003a. Revisiting Bergmann's Rule for saguaros (*Carnegiea gigantea* [Engelm.] Britt. & Rose): stem diameter patterns over space. Journal of Biogeography 30:353–359.

———. 2003b. Regional- and local-scale variations in plant distribution in the Sonoran Desert. Madroño 50:122–125.

———. 2006. Saguaro (*Carnegiea gigantea*) densities and reproduction over the northern Sonoran Desert. Physical Geography 27:505–518.

———. 2011. Cactus surface temperatures are impacted by seasonality, spines and height on plant. Environmental and Experimental Botany 74:17–21.

———. 2014. The keystone saguaro (*Carnegiea gigantea*, Cactaceae): a review of its ecology, associations, reproduction, limits, and demographics. Plant Ecology 215:581–595.

DREZNER, Z. AND T. D. DREZNER. 2016. A remedy for the overzealous Bonferroni Technique for multiple statistical tests. Bulletin of the Ecological Society of America. 97:91–98.

EVANS, L. S., C. MCKENNA, R. GINOCCHIO, G. MONTENEGRO, AND R. KIESLING. 1994. Surficial injuries of several cacti of South America. Environmental and Experimental Botany 34:285–292.

GELLER, G. N. AND P. S. NOBEL. 1986. Branching patterns of columnar cacti: influences on PAR interception and CO_2 uptake. American Journal of Botany 73:1193–1200.

LEWIS, D. A. AND P. S. NOBEL. 1977. Thermal energy exchange model and water loss of a barrel cactus, *Ferocactus acanthodes*. Plant Physiology 60:609–616.

MAJURE, L. C. AND G. N. ERVIN. 2008. The *Opuntia*s of Mississippi. Haseltonia 14:111–126.

MCAULIFFE, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. Oecologia 64:319–321.

MCAULIFFE, J. R. AND F. J. JANZEN. 1986. Effects of intraspecific crowding on water uptake, water storage, apical growth, and reproductive potential in the sahuaro cactus, *Carnegiea gigantea*. Botanical Gazette 147:334–341.

MEDEIROS, A. S. AND T. D. DREZNER. 2012. Vegetation, climate, and soil relationships across the Sonoran Desert. Ecoscience 19:148–160.

NIERING, W. A., R. H. WHITTAKER, AND C. H. LOWE. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

NOBEL, P. S. 1977. Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. Oecologia 27:117–133.

———. 1980a. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. Botanical Gazette 141:188–191.

———. 1980b. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61:1–7.

———. 1980c. Influences of minimum stem temperatures on ranges of cacti in southwestern United States and central Chile. Oecologia, 47:10–15.

———. 1983. Spine influences on PAR interception, stem temperature, and nocturnal acid accumulation by cacti. Plant, Cell & Environment 6:153–159.

———. 1988. Environmental biology of agaves and cacti. Cambridge University Press, Cambridge.

———. 2002. Physiological ecology of columnar cacti. Pp. 189–204 *in* T. H. Fleming and A. Valiente-Banuet (eds.), Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson, AZ.

NOBEL, P. S. AND E. G. BOBICH. 2002. Plant frequency, stem and root characteristics, and CO_2 uptake for *Opuntia acanthocarpa*: elevational correlates in the northwestern Sonoran Desert. Oecologia 130:165–172.

NOBEL, P. S., G. N. GELLER, S. C. KEE, AND A. D. ZIMMERMAN. 1986. Temperatures and thermal tolerances for cacti exposed to high temperatures near the soil surface. Plant, Cell & Environment 9:279–287.

NOBEL, P. S, M. E. LOIK, AND R. W. MEYER. 1991. Microhabitat and diel tissue acidity changes for two sympatric cactus species differing in growth habit. Journal of Ecology 79:167–182.

RASMUSSEN, C. 2006. Distribution of soil organic and inorganic carbon pools by biome and soil taxa in Arizona. Soil Science Society of America Journal 70:256–265.

REHFELDT, G. E., N. L. CROOKSTON, M. V. WARWELL, AND J. S. EVANS. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

SHEPPARD, P.R., A. C. COMRIE, G. D. PACKIN, K. ANGERSBACH, AND M. K. HUGHES. 2002. The climate of the US Southwest. Climate Research 21:219–238.

SHREVE, F. 1911. The influence of low temperatures on the distribution of the giant cactus. Plant World 14:136–146.

———. 1951. Vegetation and Flora of the Sonoran Desert. Volume I, Vegetation. Carnegie Institution of Washington, Publication No. 591, Washington, D.C.

STEENBERGH, W. F. AND C. H. LOWE. 1977. Ecology of the Saguaro II: reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Series No. 8., National Park Service, Washington D.C.

———. 1983. Ecology of the Saguaro III: growth and demography. National Park Service Scientific Monograph Series No. 17, National Park Service, Washington D.C.

STELFOX, J. G., AND H. G. VRIEND. 1977. Prairie fires and pronghorn use of cactus. Canadian Field Naturalist 91:282–285.

TURNER, R. M. AND D. E. BROWN. 1994. Tropical-subtropical desertlands: Sonoran Desertscrub. Pp. 180–221 *in* D. E. Brown (ed.), Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City, UT.

YEATON, R. I., R. KARBAN, AND H. B. WAGNER. 1980. Morphological growth patterns of saguaro (*Carnegiea gigantea*: Cactaceae) on flats and slopes in Organ Pipe Cactus National Monument, Arizona. Southwestern Naturalist 25:339–349.